

TAXONOMIC STUDIES ON *SEPIOTEUTHIS* BLAINVILLE (Cephalopoda: Loliginidae) FROM THE AUSTRALIAN REGION

By C. C. LU AND R. W. TAIT

Department of Invertebrate Zoology, Museum of Victoria,
285-321 Russell Street, Melbourne, Victoria 3000

ABSTRACT: *Sepioteuthis lessoniana* Lesson 1830 from Australia and *Sepioteuthis australis* Quoy & Gaimard 1832 from Australia and New Zealand are described and illustrated. A comparison is made between geographically isolated samples of each species, revealing morphologically distinct populations. *Sepioteuthis bilineata* (Quoy & Gaimard) is designated a *nomen dubium*.

Sepioteuthis was erected by Blainville (1823, p. 133) as the 'Calmars-seiches' to accommodate his new species *Loligo sepioidea*. Blainville's new group was defined as: 'Espèces dont le corps est ovale, déprimé, et dont la nageoire, fort étroite, s'étend de chaque côté, de l'extrémité antérieure à la postérieure: . . .'. The name, however, was adopted and latinised by Férussac (in d'Orbigny 1826, p. 154).

The genus was revised by Wülker (1913) and Adam (1937, 1939) and is known to occur in neritic tropical, subtropical and temperate waters worldwide, with the exception of the eastern Pacific and eastern Atlantic Oceans. Wülker included 20 species, 8 of which he considered insufficiently characterised; Adam synonymised a total of 25 names under four valid species. Those recognised by Adam (1939) are: *Sepioteuthis sepioidea* (Blainville 1823) from the east coast of Central America, particularly the Gulf of Mexico and the Caribbean Sea; *S. loliginiformis* (Rüppell & Leuckart 1828) from the Red Sea; *S. lessoniana* Lesson 1830 distributed from Hawaii to the Red Sea and from Japan to Australia; and *S. australis* Quoy & Gaimard 1832 from Australia and New Zealand.

Sasaki (1929) offered the following definition of the genus and although his work included only *S. lessoniana*, he significantly extended the original definition: 'Body conico-cylindrical, ending rather bluntly behind. Fins enormous, marginal; at maturity, extending the whole length of mantle; both together ovate. Hectocotylisation affecting the distal part of left ventral arm. Spermatheca present on the ventral part of buccal membrane, containing internally a pair of ramified seminal receptacles'.

Five species of *Sepioteuthis* have been reported from Australian and New Zealand waters: *Sepioteuthis lessoniana* (Gray 1849, Brazier 1892); *S. bilineata* (Quoy & Gaimard 1832, Hutton 1880, Kirk 1884, Dell 1952); *S. australis* (Quoy & Gaimard 1832, McCoy 1883, von Martens 1889, Whitelegge 1889, Brazier 1892, Hedley 1915, Berry 1918, Verco & Cotton 1928, Cotton & Godfrey 1940, Allan 1959); *S. mauritiana* (Brazier 1892, Meyer 1909), and *S. lunulata* (Brazier 1892). *Sepioteuthis lessoniana* has been reviewed in detail by Adam (1939). Gray's (1949) record from New Zealand is the only record from that country and may be regarded as doubtful (Dell 1952). Australian species are com-

pared with material from Indonesia and the Philippines in the present study.

Sepioteuthis bilineata (Quoy & Gaimard 1832) was poorly described from a single specimen from Western Port, Victoria, Australia, which was later lost (Quoy & Gaimard 1832, p. 68). Subsequent usage of the name applied only to the original description until Hutton (1880) introduced it into New Zealand literature for a specimen he had previously designated *S. major* (Hutton 1873). The name *S. bilineata* was adopted for the common species of *Sepioteuthis* in New Zealand by Kirk (1884), Suter (1913), Powell (1946, 1979) and Dell (1952). Adam (1939) suggested that *S. bilineata* was a *species dubium* but Dell (1952) considered it the senior synonym of *S. australis*, on the grounds that *S. bilineata* has page priority.

Sepioteuthis australis was well described and illustrated, also from a specimen from Western Port. It is found to be conspecific with material from New Zealand and the geographic variation within the species is discussed.

Sepioteuthis mauritiana and *S. lunulata* are both synonyms of *S. lessoniana* (Adam 1939, p. 30). However, Meyer's (1909) description of a specimen of *S. mauritiana* from Albany, southwestern Australia is considered by Adam (1939, p. 28) to be referable to *S. australis*.

MEASUREMENTS AND ABBREVIATIONS

Measurements (in millimetres) and abbreviations used in this paper are defined below. Indices unless otherwise specified are expressed as a percentage of dorsal mantle length and are denoted by the final initial I, e.g. $MW1 = MW/ML \times 100$. Beak measurements follow Clarke (1962) with the exception of baseline length (BL) and depth (D).

ML —	dorsal mantle length, measured from the anterior most point of the mantle to the posterior tip.
VML —	ventral mantle length, measured in the ventral mid line.
MW —	greatest mantle width.
HL —	head length, measured from the junction of the first pair of arms to the anterior end of the nuchal cartilage.

HW—	greatest head width, measured across the eyes.
FL—	greatest length of fins, measured in the mid line.
FW—	greatest width across both fins.
AL _{I, II, III, IV} —	arm length, of each right arm measured from the base of the first proximal sucker to tip of arm. (Arm I, dorsal; II, dorsal-lateral; III, ventro-lateral; IV, ventral).
HA—	hectocotylised arm length.
HC—	length of hectocotylus. Index expressed as a percentage of the hectocotylised arm length.
TL—	total length of tentacular stalk and club.
CL—	length of right tentacular club from the proximal most carpal sucker to the club tip.
AS _{I, II, III, IV} —	internal diameter of sucker rings of the largest sucker on each right arm.
CS—	internal diameter of the largest sucker ring on the right club.
GW—	greatest width of gladius.
RL—	length of free rachis, measured from anterior end of gladius to the point where the anterior edge of the vane joins the rachis.
RW—	width of rachis where it joins the vane.
SL—	spermatophore length, excluding cap thread.
SRI—	spermatophore sperm reservoir index, length of sperm reservoir as a percentage of the spermatophore length.
SWI—	spermatophore width index, greatest width of spermatophore as a percentage of the spermatophore length.
NL—	nidamental gland length.
ROL—	beak rostral length.
ROW—	beak rostral width.
WL—	beak wing length.
BL—	beak baseline length, measured in mid line between anterior tip of wing and posterior tip of lateral wall.
D—	beak depth, measured in vertical plane between rostral tip and end of wing.
HdL—	beak hood length.
CrL—	beak crest length.
LWL—	beak lateral wall length.

All measurements except suckers and beaks were made to the nearest 0.1 mm and rounded to the nearest millimetre. Sucker diameters and beaks were measured to the nearest 0.05 mm and rounded to the nearest 0.1 mm. The described specimens are housed in the collections of the Museum of Victoria, Melbourne (NMV), the National Museum of New Zealand, Wellington,

New Zealand (NMNZ), and the Zoologisk Museum, University of Copenhagen, Denmark (ZMC). Other repositories are indicated by WAM—Western Australian Museum, Perth, and MNHP—Muséum National d'Histoire Naturelle, Paris.

Regression analyses and comparisons between lines were done by the method given in Zar (1974, p. 228). Dates of publication of species described in Férussac and d'Orbigny (1835-48) are taken from Winckworth (1942).

Genus *Sepioteuthis* Blainville 1823

1828 *Chondrosepia* Rüppell & Leuckart, p. 21.

TYPE SPECIES: *Loligo sepioidea* Blainville 1823.

DIAGNOSIS: Body stout, slightly flattened dorsoventrally, tapers to a blunt point. Fins of adults and subadults large, muscular, extend for nearly the entire mantle length, continuous around posterior margin. Hectocotylisation affects distal portion of left ventral arm. Photophores lacking.

Sepioteuthis lessoniana Lesson 1830

Figs 1-4, 8a

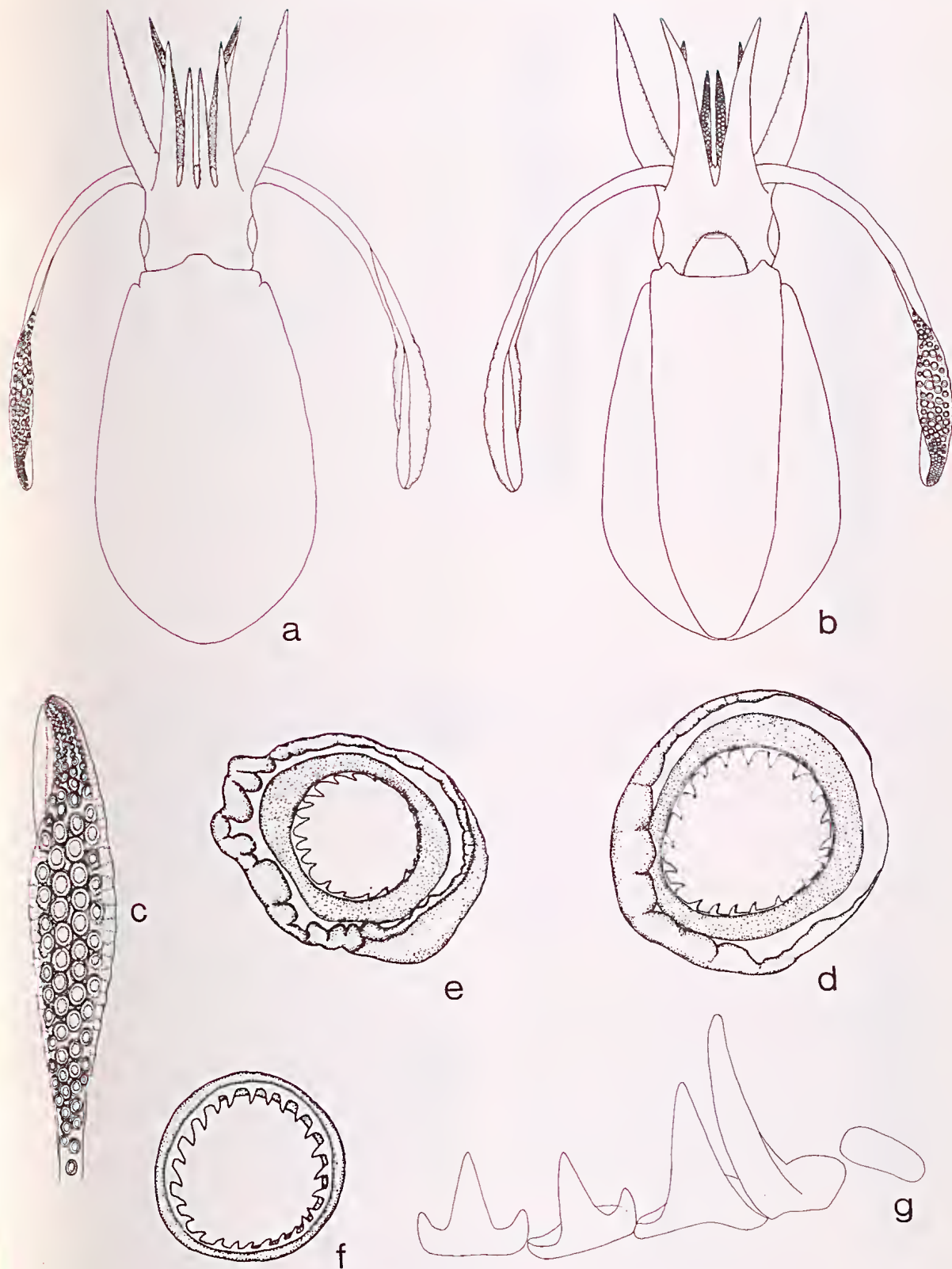
- 1826 *Sepioteuthis lessoniana* Férussac in d'Orbigny, p. 155. (*nomen nudum*)
 1830 *Sepioteuthis lessoniana* Lesson, p. 244, pl. 2.
 1832 *Sepioteuthis guinensis* Quoy & Gaimard, p. 72, pl. 3, figs 1-7.
 1832 *Sepioteuthis lunulata* Quoy & Gaimard, p. 74, pl. 3, figs 8-13.
 1832 *Sepioteuthis mauritiana* Quoy & Gaimard, p. 76, pl. 4, figs 2-6.
 1835 *Sepioteuthis dorensis* Férussac & d'Orbigny, *Sepioteuthis* pl. 3, fig. 2.
 1848 *Sepioteuthis sinensis* Férussac & d'Orbigny, p. 304.
 1852 *Sepioteuthis arctipinnis* Gould, p. 479, p. 49, fig. 593.
 1881 *Sepioteuthis brevis* Owen, p. 137, pl. 26, fig. 1.
 1884 *Sepioteuthis neoguinaica* Pfeffer, p. 4, pl. 1, fig. 2.
 1896 *Sepioteuthis indica* Goodrich, p. 5, pl. 1, figs 9-19.
 1898 *Sepioteuthis sieboldi* Joubin, p. 27.
 1913 *Sepioteuthis malayana* Wülker, p. 478, fig. 7.
 1928 *Sepioteuthis kremphi* Robson, p. 28, figs 13-16.

DIAGNOSIS: Fins widest in their posterior third. Buccal membrane well developed, suckers present on all lappets.

MATERIALS EXAMINED: See APPENDIX 5.

DESCRIPTION: *Mantle* stout (MW1 24-35), tapers to a blunt tip posteriorly; anterior dorsal lobe broad, rounded; ventrolateral lobes low, pointed. *Fins* large,

Fig. 1—*Sepioteuthis lessoniana* Lesson; male, NMVF31555, 155 mm ML. a, dorsal view. b, ventral view. c, left tentacle club. d, largest median manal sucker of club. e, largest marginal manal sucker of club. f, largest sucker ring from right third arm. g, radula. (d-f orientated distal aspect to top of page).



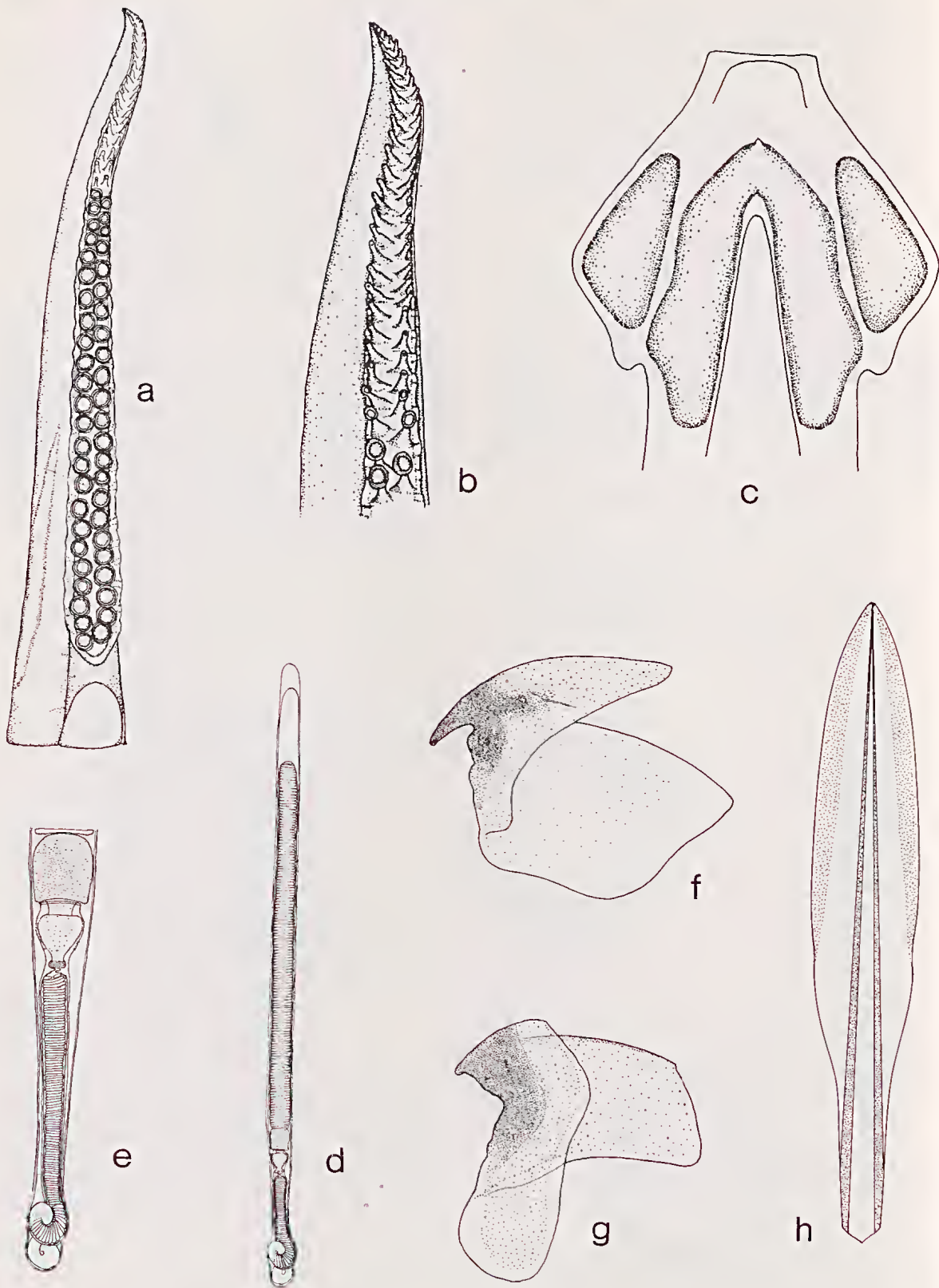


TABLE 1
MEANS, STANDARD DEVIATIONS AND RANGES OF INDICES OF *Sepioteuthis lessoniana* FROM AUSTRALIA

Index	n	MALES			n	FEMALES		
		Mean	S.D. (n-1)	Range		Mean	S.D. (n-1)	Range
ML(mm)				104-356				85-250
MWI	13	30.3	2.7	24-35	7	32.3	3.4	26-35
HLI	13	23.1	3.4	17-29	7	23.6	1.1	22-25
HWI	13	24.6	2.7	21-31	7	24.8	1.7	22-27
FLI	13	90.5	2.5	86-94	7	90.6	2.6	87-93
FWI	13	62.7	7.6	53-80	7	64.9	7.0	58-77
FL/FW	13	146.2	16.7	115-168	7	140.7	12.9	121-157
AL _I I	12	29.6	2.4	27-33	7	27.7	2.2	25-31
AL _{II} I	13	39.0	3.5	34-48	7	37.0	3.9	32-43
AL _{III} I	13	47.1	2.7	44-53	6	44.6	3.9	40-49
AL _{IV} I	12	41.8	3.4	36-48	7	41.4	2.9	37-46
HAI	11	42.3	2.9	37-51				
HCI	11	29.3	2.5	25-34				
TLI	13	102.7	15.7	82-135	7	97.9	14.8	76-115
CLI	13	39.3	4.3	33-44	7	38.6	5.4	35-49
AS _I I	13	0.83	0.08	0.6-0.9	7	0.86	0.11	0.8-0.9
AS _{II} I	13	1.01	0.09	0.8-1.1	7	1.02	0.08	0.9-1.1
AS _{III} I	13	1.22	0.10	1.0-1.3	7	1.19	0.12	1.0-1.3
AS _{IV} I	13	0.86	0.07	0.7-1.0	7	0.89	0.05	0.8-0.9
CSI	13	1.64	0.28	1.0-1.9	7	1.46	0.24	1.2-1.8
GW1	13	18.3	1.2	15-20	7	19.5	1.8	18-22
RL1	13	19.3	1.7	16-22	7	16.5	2.2	13-20
RW1	13	6.54	0.43	5.2-7.1	7	6.60	0.51	5.9-7.4
SL(mm)	11			6.8-14.5				
SLI	11	4.84	0.60	4.0-5.8				
SR1	11	75.4	1.9	72-79				
SW1	11	4.61	0.40	3.8-5.1				

continuous posteriorly, extend for 86-94% of ML, less in very small specimens, widest in their posterior third (Fig. 1a, b); anterior lobes small, posterior margins well rounded, anterolateral margins only slightly convex. Funnel large, very stout; dorsal funnel organ (Fig. 2c) with broad limbs, expanded in anterior and posterior thirds, taper to blunt tips posteriorly; anterior end very blunt, small apical papilla present; ventral pads of funnel organ about two-thirds length of dorsal organ, broader posteriorly. Funnel valve subterminal, rounded with steep shoulders.

Head and eyes large, olfactory crest prominent, preocular pore present adjacent to base of third arm. Arms moderately long, order III, IV, II, I, robust, tapering evenly to fine tips. Arm I triangular in section with an aboral keel; Arm II with an aboral keel along its entire length; Arm III broad, with a thick, low aboral swimming keel; Arm IV lacks an aboral keel, broad tentacular sheath present dorsally, this may be distorted and narrowed proximally by ridges in the sheath musculature (Fig. 2a). Trabeculate protective membranes on Arms I-III very well developed, trabeculae arise between sucker bases, become diffuse at edge of

membranes. Both membranes on Arm I equal in height, dorsal membranes on Arms II and III lower than ventral membranes. Membranes on Arm IV low, ventral membrane lower, edges scalloped; trabeculae weaker than on Arms I-III. Arm suckers increase in size from proximal end distally, largest at one quarter of arm length from proximal end, diminish evenly in size distally becoming minute at tip; arm suckers lack fleshy protuberances seen on club manal suckers. Largest arm sucker rings on all arms with 17-28 teeth on complete circumference; distal teeth long, acutely pointed; proximal teeth small, blunt. Teeth on distal sucker rings fewer, often truncate (Fig. 1f).

Left ventral arm of males *hectocotylied* (Fig. 2a, b) by modification of distal 25-34%; 22-26 pairs of suckers modified into long, fleshy papillae slightly larger in dorsal row; each papilla has a minute sucker at its apex, suckers on distal papillae lack sucker rings. On proximal portion of arm, 23-31 pairs of suckers remain unmodified; each sucker ring bears 20-28 teeth similar to those on other arms. Trabeculate protective membranes on unmodified portion of arm similar to those on right ventral arm; along modified portion ventral membrane

Fig. 2—*Sepioteuthis lessoniana* Lesson. a-e, male, NMVF31555, 155 mm ML. a, left ventral arm. b, hectocotylied portion of left ventral arm. c, funnel organ. d, spermatophore. e, oral end of spermatophore. f-g, male, NMVF31557, 356 mm ML. f, upper beak. g, lower beak. h, gladius; male, NMVF31576, 217 mm ML.

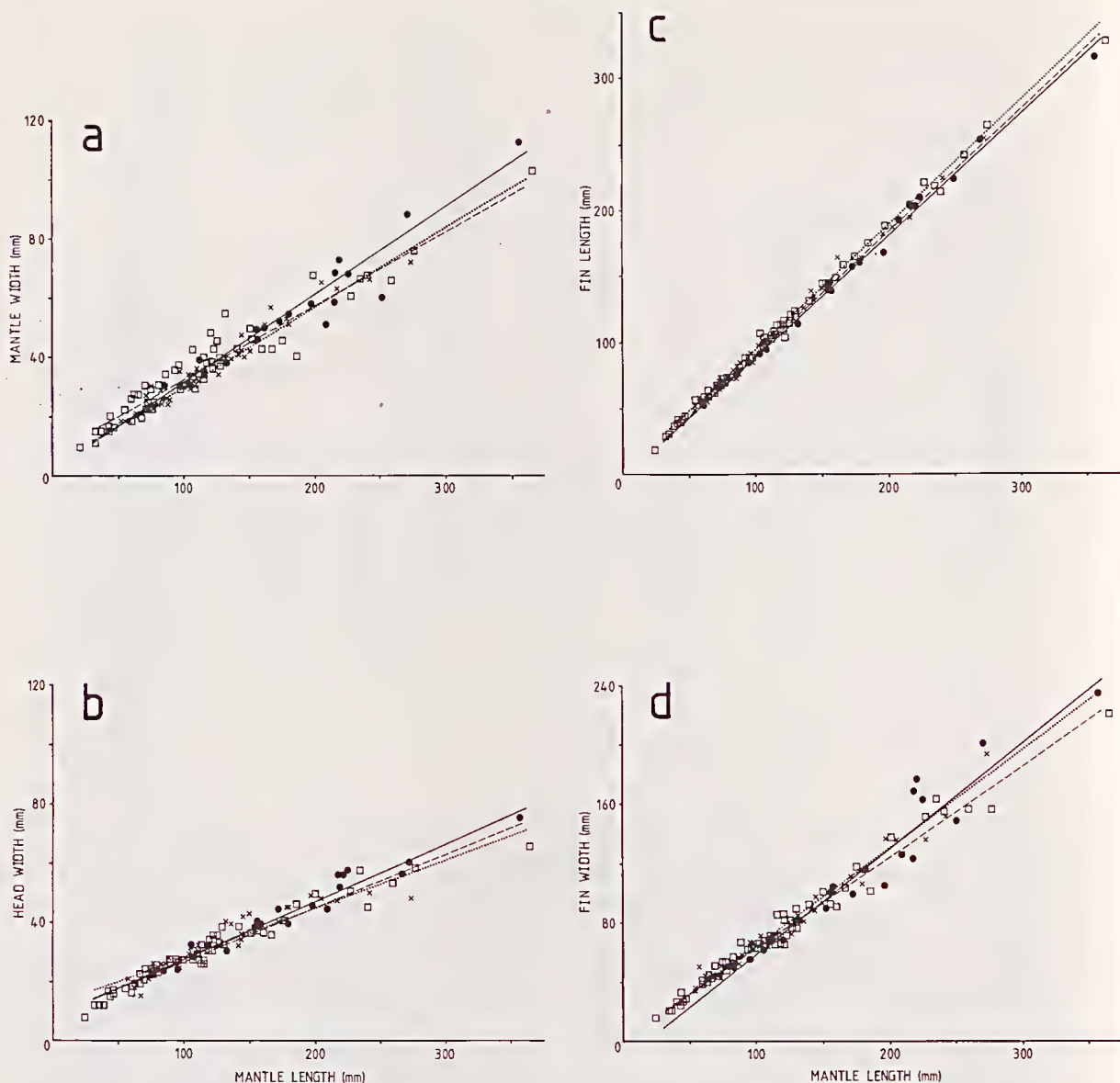


Fig. 3—Comparison of morphological parameters of *Sepioteuthis lessoniana* from Australia, Indonesia and the Philippines.

Australian sample—solid lines, solid dots.

Indonesian sample—dashed lines, hollow squares (measurements from Adam 1939).

Philippines sample—dotted lines, crosses (measurements from Voss 1963 and NMVF31764).

Regression data and comparisons of lines are given in Table 2.

continues to arm tip, dorsal membrane continues for only one-third to one-half hectocotylus length. *Tentacles* moderately long, robust; stalks naked. Clubs large, expanded (Fig. 1c); carpus and manus not distinct from each other, dactylus slender. Suckers on carpus biserial for proximal 1-2 pairs then tetraserial; manal suckers moderately large, possess finger-like fringes on outer margins, better developed on marginal suckers (Fig. 1d, e); median suckers 1.1-1.5 times diameter of marginal suckers; dactylus suckers small, decrease in

size from ventral to dorsal rows; distal tip slightly expanded, small naked patch present between median sucker rows at tip. Aboral swimming keel arises along the carpus, expands distally and terminates abruptly at tip; keel thickened along attachment to club. Trabeculate protective membranes arise from the proximal portion of the carpus, well developed; dorsal membrane terminates at the proximal portion of the dactylus; ventral membrane continues along dactylus, terminates at club tip; trabeculae on both membranes

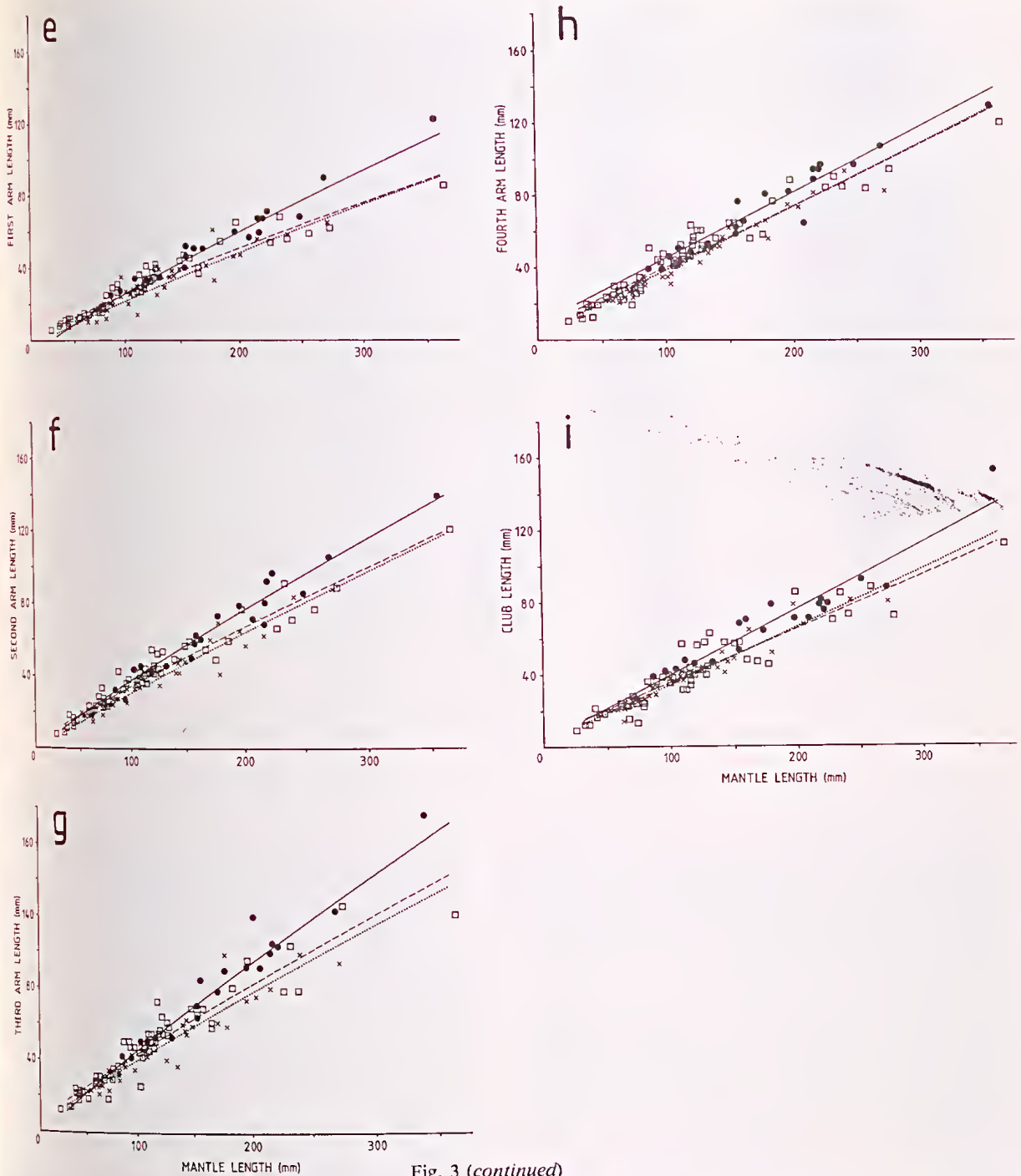


Fig. 3 (continued)

arise between sucker stalks, broad, strong, slightly diffuse at edges of membranes.

Sucker rings of the carpus with 13-23 acutely pointed teeth, longer and more acute on distal margins; manal sucker rings with 13-24 strong, sharp, well spaced teeth, larger and more acute on distal margins of median suckers and on outer margins of marginal suckers. Sucker rings of dactylus with 15-23 sharp teeth, teeth

larger on ventral suckers, fewer on distal suckers; suckers of terminal expansion of dactylus with low, rounded teeth or lacking dentition. *Buccal membrane* with seven lappets, supported by strong connectives, ventral lappets generally lower than others; each lappet bears 0-10 small suckers, fewer on ventral lappets; each sucker ring with 15-25 minute, truncate teeth, larger on distal margins. Buccal seminal receptacle present on oral

TABLE 2
COMPARISON OF MORPHOLOGICAL PARAMETERS OF *Sepioteuthis lessoniana* FROM AUSTRALIA, INDONESIA
AND THE PHILIPPINES

Regression data relating to Fig. 3. $y = bx + a$; n = no. of individuals per sample; b = regression coefficient; a = vertical intercept; R^2 = coefficient of determination; sig. diff. = significant difference between the lines indicated by the parentheses, with respect to slope or elevation. Regression coefficients in all cases are significant at the 0.1% level.

Ref. Fig. 3	Function	Sample	n	b	a	R^2	sig. diff.
a	MW-ML	Indon.	56	0.2491	7.2989	0.9243	
		Aust.	20	0.2949	2.1962	0.9222	$p < 0.05$ (slope)
		Philipp.	41	0.2634	4.2409	0.9669	$p < 0.05$ (elev.)
b	HW-ML	Indon.	56	0.1785	8.7720	0.9419	
		Aust.	20	0.1957	8.0775	0.9458	$p < 0.02$ (elev.)
		Philipp.	34	0.1662	11.4587	0.8699	N.S.
c	FL-ML	Indon.	56	0.9275	-0.2117	0.9966	
		Aust.	20	0.9234	-2.5962	0.9950	$p < 0.01$ (elev.)
		Philipp.	41	0.9200	0.6374	0.9972	$p < 0.02$ (elev.)
d	FW-ML	Indon.	56	0.6089	1.9452	0.9773	
		Aust.	20	0.7194	-13.4932	0.9206	$p < 0.005$ (slope)
		Philipp.	41	0.6512	-0.5959	0.9779	N.S.
e	AL _I -ML	Indon.	56	0.2464	1.2267	0.9322	
		Aust.	19	0.3430	-9.1813	0.9598	$p < 0.001$ (slope)
		Philipp.	41	0.2586	-2.8803	0.8940	$p < 0.001$ (slope)
f	AL _{II} -ML	Indon.	55	0.3227	2.8631	0.9428	
		Aust.	20	0.3933	-2.2372	0.9565	$p < 0.002$ (slope)
		Philipp.	41	0.3317	-1.4673	0.8772	$p < 0.05$ (slope)
g	AL _{III} -ML	Indon.	56	0.3814	5.4510	0.9347	
		Aust.	19	0.4894	-4.2879	0.9744	$p < 0.001$ (slope)
		Philipp.	41	0.3684	3.5439	0.9010	$p < 0.001$ (slope)
h	AL _{IV} -ML	Indon.	56	0.3383	6.6125	0.9185	
		Aust.	19	0.3640	8.4895	0.9604	$p < 0.002$ (elev.)
		Philipp.	41	0.3506	3.5541	0.9253	$p < 0.001$ (elev.)
i	CL-ML	Indon.	53	0.2972	5.9639	0.9036	
		Aust.	20	0.3643	3.3195	0.9107	$p < 0.02$ (slope)
		Philipp.	38	0.3198	2.7019	0.9370	$p < 0.001$ (elev.)

surface between ventral lappets of females, very well developed; large white, glandular organ lies just under surface of membrane, opens through a narrow, elongate aperture; small papilla present at aboral end of aperture. Rostrum of *upper beak* (Fig. 2f) sharply pointed, long, curved; width slightly less than or equal to length; rostral margin and tip dark brown to black, dark pigmentation expanded posteriorly from jaw angle, remaining area of rostrum and hood lightly pigmented. Hood length about 3.5-6.0 times rostral length; wing length about 1.5-2.3 times rostral length, cutting edge of wing irregular, a large tooth present near jaw angle. Crest curved, lateral wall large, lightly pigmented anteriorly (at least on specimens larger than 104 mm ML) posterior margin with a shallow indentation, posterior margin of lateral wall unpigmented. Rostrum of *lower beak* (Fig. 2g) long, pointed, black cutting edge of rostrum straight, irregularly serrated, rostral width slightly greater than or equal to rostral length; wing length about 2.3-3.7 times rostral length; cutting edge of wing straight, irregularly serrated; margin of wing unpigmented, remaining area of wing lightly pigmented. Hood heavily pigmented anteriorly, black, lightly pigmented posteriorly. Crest curved, crest length about

3.5-4.0 times rostral length; lateral wall length about 4-5 times rostral length, lightly pigmented with transparent margins. *Radula* (Fig. 1g) with seven transverse rows of teeth; rhachidian tooth stout with straight edges, lateral cusps high, blunt; first lateral stout, similar length to rhachidian, lateral cusps high, blunt; second lateral slightly curved, stout, 1.5-2.0 times length of rhachidian, no cusps; third lateral curved, stout, 2.0-2.5 times length of rhachidian, tip blunt; marginal plates elongate, narrower in their outer third. *Gladius* (Fig. 2h) broad, vane widest in its posterior third, conspicuously dilated posteriorly to attachment of funnel adductor muscles; vane thickened in a broad band immediately median to edges, extending from attachment of funnel adductor muscles to posterior tip, vane edge not thickened. Free rachis short, longer in small specimens, broad, strong; median groove rounded, supported by strongly thickened lateral rods for length of gladius. *Spermatophores* of Australian specimens (Figs 2d, e, 4a, b) small, sperm mass comprises 72-79% of total length. Cement body clearly bipartite; aboral end rounded, stout, connected to oral end by a narrow neck; oral end flask shaped with distinct shoulders tapering evenly to a small, dark terminal dilation. Middle tunic spirally

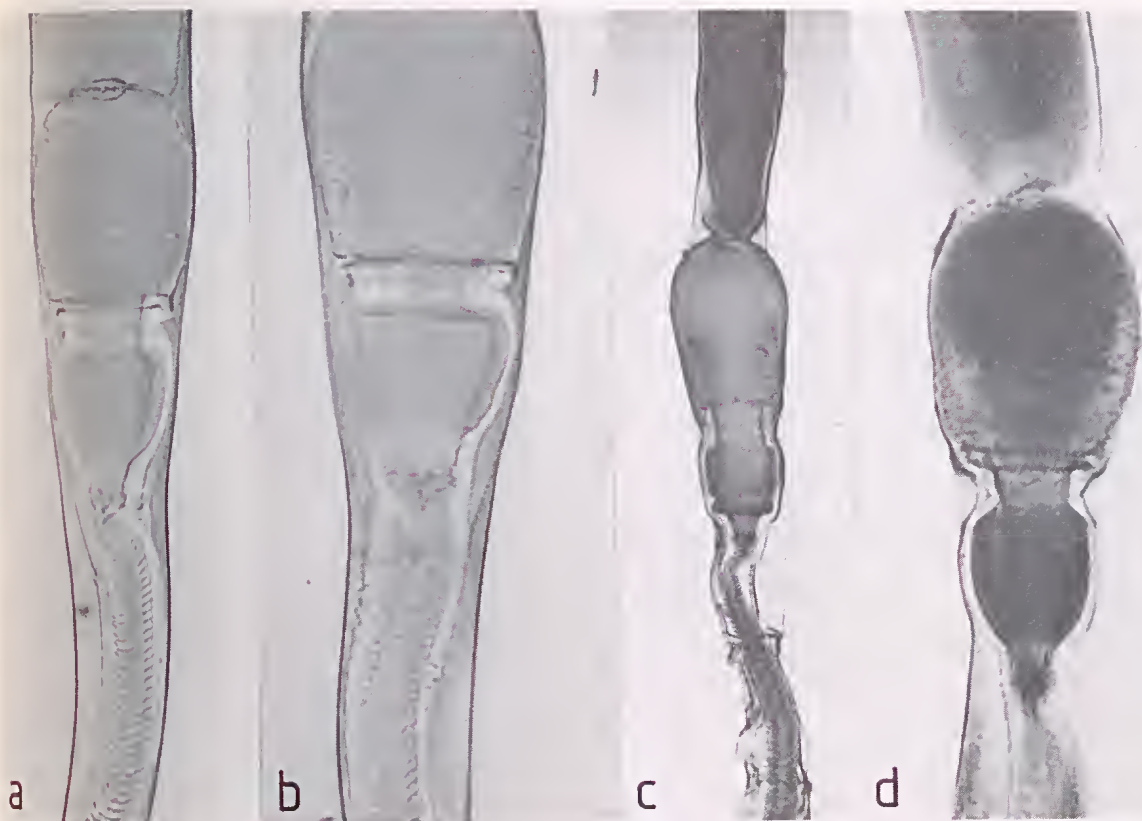


Fig. 4—*Sepioteuthis lessoniana* Lesson. Geographic variation in spermatophore cement bodies from Australia, Philippines and Vietnam. a, NMVF31552, 118 mm ML, N.E. Australia. b, NMVF31555, 155 mm ML, N.W. Australia. c, NMVF31764, 273 mm ML, Philippines. d, ZMC, 112 mm ML, Vietnam.

sculptured along oral end of cement body, forms a distinct shoulder opposite cement body neck; ejaculatory apparatus tightly coiled, forms several large coils in the oral swelling of spermatophore. Specimens in isopropyl alcohol cream coloured; dorsal surface of body and fins closely covered in large purplish chromatophores, in some specimens a darker median line or irregularly placed, short transverse dashes are present; chromatophores on ventral body surface less concentrated, absent on ventral fin surfaces. Head and aboral aspects of arms and tentacles also closely covered with chromatophores, less concentrated ventrally; dark patch present dorsal to each eye. No photophores present on this species. The smallest male examined which had well developed spermatophores present in the needhams sac was 120 mm ML, hectocotylation is evident in immature males as small as 71 mm ML. The nidamental glands of females begin rapid enlargement from 160-200 mm ML.

HOLOTYPE: Not traced. Muséum National d'Histoire Naturelle, Paris?

TYPE LOCALITY: 'Le havre de Doréry'=(?) Dore Bay, West Irian, approximately 0°51'S., 134°01'E.

DISTRIBUTION: A neritic species widely distributed in the Indian and Pacific Oceans, from Japan (Okutani 1973)

to Australia, and the Red Sea (Adam 1973) to the Hawaiian Islands (as *S. arctipinnis*) (Berry 1912); not recorded from the eastern Pacific coast of America. Records from New Zealand by Gray (1849, p. 80) not confirmed. In Australia this species is recorded from northern coastal waters to depths of 110 m (Fig. 8a). Southern most records are: eastern coast 27°12'S. (NMVF31611); western coast 28°48'S. (WAM1420-83).

GEOGRAPHIC VARIATION: The Australian sample could be separated morphometrically from the Indonesian and Philippine samples by comparison of any of the parameters: mantle width, fin length, fin width, lengths of Arms I-IV and tentacle club length. Head length and gladius width were the only parameters tested which did not show a separation. The best separation of Australian and Asian samples was found by comparison of arm lengths (Fig. 3e-h). In general, mature specimens from Australia are slightly broader, a difference reflected in mantle, head and fin width, and the arms and tentacle clubs are slightly longer.

Differences in the shape of cement body of the spermatophore were also apparent. Specimens from the east and west coasts of Australia are identical, the cement body has a flask shaped oral end, evenly tapered (Fig. 4a, b). Specimens from the Philippines (Fig. 4c) have a

larger aboral part to the cement body; the oral part is stout with a slight constriction at half its length, a well developed shoulder is present orally, adjacent to the terminal dilation. The single specimen examined from Vietnam (Fig. 4d) is similar to Australian examples but has a larger aboral part to the cement body and less marked aboral shoulders on the oral part.

REMARKS: *Sepioteuthis lessoniana* from Australia matches closely with the detailed descriptions of Sasaki (1929, p. 127), Adam (1939, p. 2) and Voss (1963, p. 77). The transverse dashes seen on the dorsal surface of some specimens were described by Ikeda (1933) and Adam (1938) as a secondary sexual characteristic of males. These markings were only observed on Australian male specimens but the corresponding markings described by the above authors on females were not observed. The morphometric variation shown by this species was noted by Adam (1939), who examined a total of 84 specimens and gave detailed measurements for 59, from various Indonesian localities, some from as close to Australia as Timor. This is the first time however, that material has been statistically compared from widely separated geographic locations where some isolation may be expected. The results indicate that the Australian material may belong to a population morphologically separable from its nearest northern neighbours and this is supported by differences in spermatophore morphology. This may be due to distance factors alone, but areas of deeper water separating sample localities would also have isolating effects over shorter distances on a neritic species. Further analysis of variation on a finer scale, such as within the large ranges of the species within Australian and Indonesian waters would require a much larger sample than that available to the present study.

Sepioteuthis australis Quoy & Gaimard 1832

Figs 5-7, 8b, 9-10

1832 *Sepioteuthis australis* Quoy & Gaimard, p. 77, pl. 4, fig. 1.

1873 *Sepioteuthis major* Hutton, p. 3 (non Gray, 1828).

1880 *Sepioteuthis bilineata* Hutton, p. 3.

1909 *Sepioteuthis mauritiana*; Meyer, p. 329, figs 1-2 (non Quoy & Gaimard, 1832).

DIAGNOSIS: Fins widest at about half their length; buccal membrane well developed, suckers present on all lap-pets. Restricted to southern Australia and New Zealand waters.

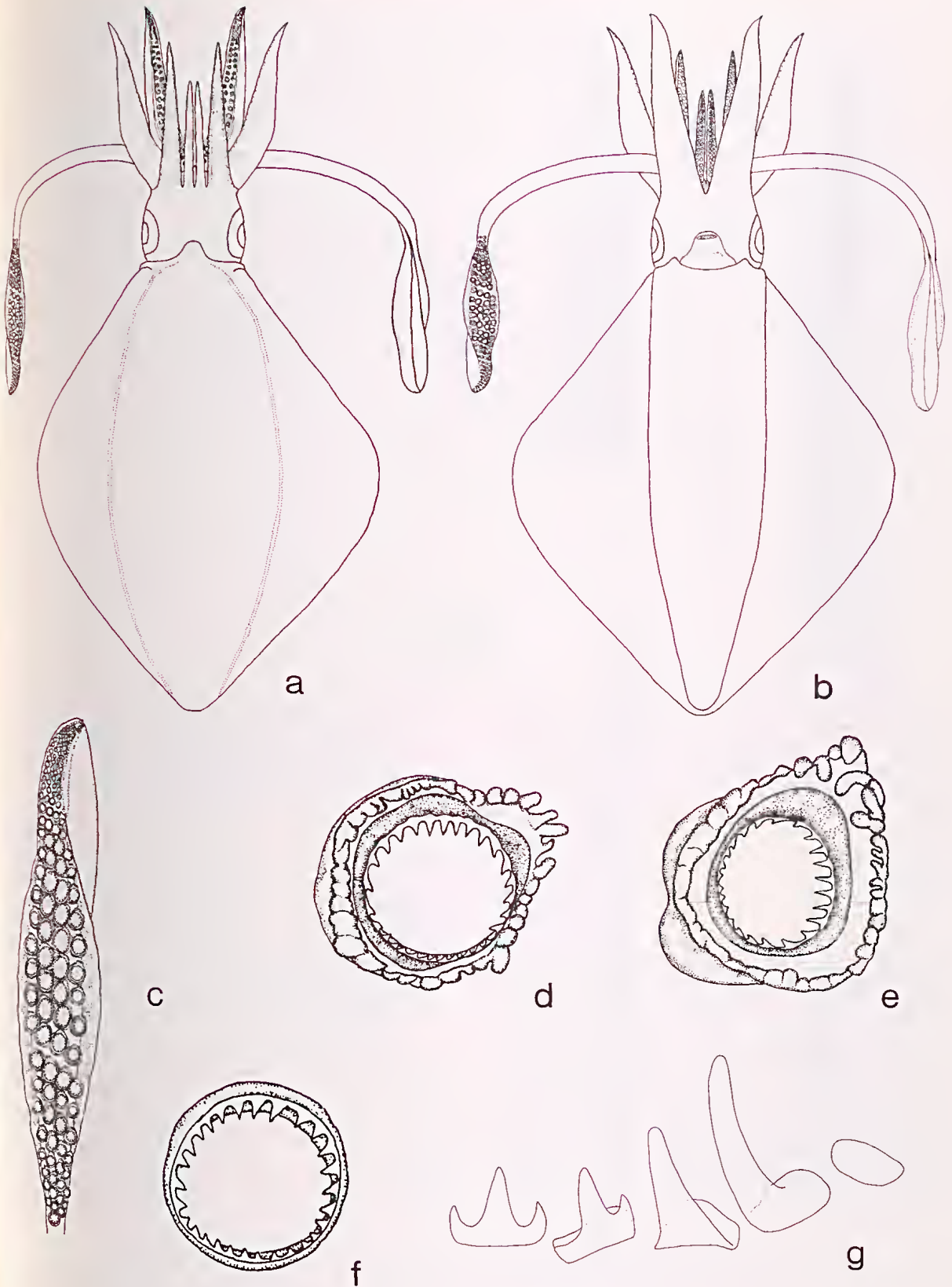
MATERIALS EXAMINED: See APPENDIX 6.

DESCRIPTION: *Mantle* stout, broader in New Zealand specimens, tapers to a blunt tip posteriorly; anterior dorsal lobe prominent, rounded; ventrolateral lobes low, pointed. *Fins* large, rhombic (Fig. 5a, b) broadest at midpoint, continuous posteriorly; extend for 78-96%

of mantle length, less in very small specimens; anterolateral and posterolateral margins straight or slightly convex, anterior lobes small. *Funnel* large, broad, strongly tapered, dorsal funnel organ (Fig. 6c) with broad limbs, tapering posteriorly to a blunt tip, becoming narrow anteriorly with a raised fleshy pad at tip and a well developed apical papilla. Ventral pads about half length of dorsal organ, dorsal margin nearly straight, pads widest just posterior to midpoint; funnel valve subterminal, rounded. *Head* and eyes large, olfactory crest prominent, preocular pore present adjacent to base of third arm. *Arms* moderately long, all robust, order III, IV, II, I or IV, III, II, I, taper evenly to fine tips. Arm I triangular in section with a well developed aboral keel disappearing proximally; Arm II with an aboral keel along its entire length. Arm III broad, triangular in section well developed aboral keel present along entire length. Arm IV lacks an aboral keel, dorsally a broad tentacular sheath is present, somewhat distorted proximally in large specimens by muscular ridges in the sheath (Fig. 6a), ventrally a low flange is present on distal two-thirds of arm. Trabeculate protective membranes on Arms I-III well developed, dorsal and ventral membranes equal in height; trabeculae arise between sucker bases, strong at base, become diffuse at edges of membranes. Membranes on Arm IV less well developed, slightly scalloped at edges, ventral membrane lower than dorsal membrane; trabeculae weaker than on Arms I-III. *Suckers* largest at about one-quarter of arm length from proximal end, diminish evenly in size distally, becoming minute at distal tip; largest suckers on all arms slightly smaller in New Zealand specimens; arm suckers lack fleshy protuberances seen on club manal suckers. Largest arm sucker rings on Arms I-IV with 18-32 well spaced teeth on complete circumference; distal teeth moderately short, sharp or peg like; proximal teeth small, conical or blunt. Teeth on distal sucker rings of all arms fewer, truncate or rounded. Left ventral arm of males *hectocotylised* by modification of distal 18-22% (Fig. 6a, b); 24-28 pairs of suckers in this region modified into long, fleshy papillae slightly larger in the dorsal row, each with a minute sucker at its apex. Terminal portion of hectocotylus on large, mature males attenuate, weak; distal 9-10 pairs of papillae greatly reduced, suckers at tips similar size to most distal suckers on right ventral arm; tentacular sheath becomes very weak and ventral flange disappears along attenuate tip. Proximal portion of the arm with 32-41 pairs of unmodified suckers, sucker ring dentition similar to that of other arms. Trabeculate protective membranes along unmodified portion of arm similar to those on right ventral arm; along modified portion membranes are reduced, strongly scalloped, fused to papillae; continuing to distal tip on both sides.

Tentacles moderately long, robust, stalks naked. *Clubs* (Fig. 5c) large, expanded, slightly smaller in New

Fig. 5—*Sepioteuthis australis* Quoy & Gaimard; male, NMVF30876, 214 mm ML. a, dorsal view. b, ventral view. c, right tentacular club. d, largest median manal sucker of club. e, largest marginal sucker of club. f, largest sucker ring from third right arm. g, radula. (d-f orientated distal aspect to top of page).



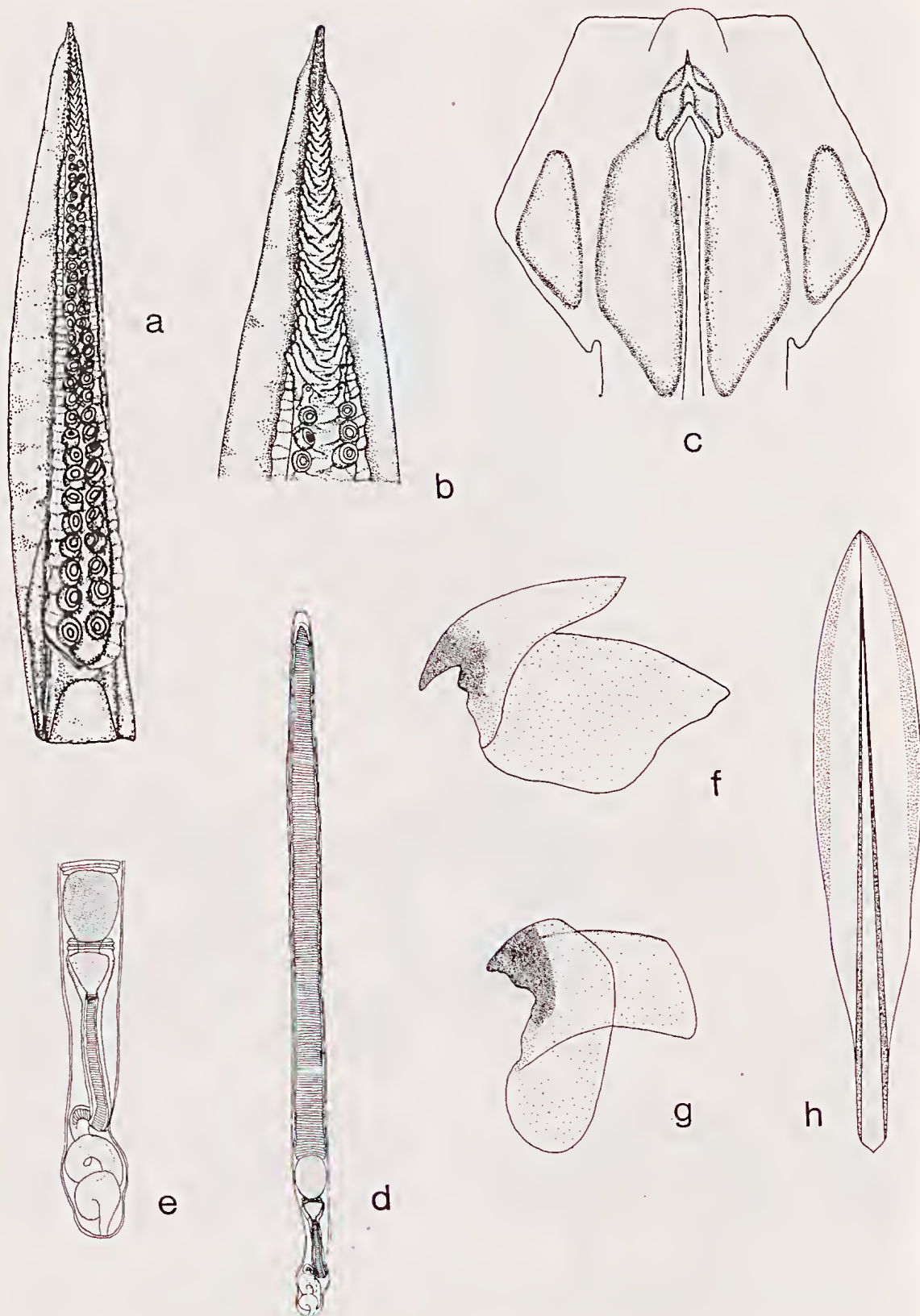


TABLE 3
MEANS, STANDARD DEVIATIONS AND RANGES OF INDICES OF *Sepioteuthis australis* QUOY & GAIMARD FROM AUSTRALIA AND NEW ZEALAND

Index	n	Mean	S.D. (n - 1)	Range	n	Mean	S.D. (n - 1)	Range
ML(mm)	17			33-355	15			43-256
MW1	17	29.4	4.7	23-39	15	29.8	4.6	23-40
HL1	17	21.9	4.4	17-30	15	22.3	2.1	20-27
HW1	17	26.7	4.9	18-34	15	26.8	3.5	22-33
FL1	17	88.1	4.3	78-93	15	89.3	3.1	84-96
FW1	17	74.3	6.7	65-89	15	75.5	7.2	62-87
FL/FW	17	119.4	9.8	102-135	15	119.5	12.8	102-146
AL _I 1	17	24.0	3.9	16-30	15	24.1	2.2	21-29
AL _{II} 1	17	34.2	3.9	26-29	15	34.5	2.7	31-41
AL _{III} 1	17	41.6	5.8	33-52	15	41.3	3.7	33-48
AL _{IV} 1	17	39.5	5.9	30-49	15	40.8	3.5	36-48
HA1	4	37.5	3.1	35-41				
HC1	4	20.3	1.5	18-22				
TL1	17	95.2	23.7	65-132	15	90.1	24.1	64-128
CL1	17	32.2	4.1	26-42	15	32.4	3.4	27-38
AS _I 1	17	0.51	0.10	0.3-0.7	15	0.54	0.07	0.4-0.7
AS _{II} 1	17	0.72	0.13	0.5-0.9	15	0.75	0.10	0.6-0.9
AS _{III} 1	17	0.85	0.15	0.6-1.2	15	0.89	0.10	0.7-1.1
AS _{IV} 1	17	0.61	0.12	0.4-0.8	15	0.65	0.06	0.6-0.8
CS1	17	1.15	0.32	0.6-1.7	15	1.27	0.26	0.9-1.8
GW1	17	18.6	1.8	16-21	15	18.3	2.0	15-22
RL1	17	19.3	1.9	16-24	14	18.6	1.8	16-22
RW1	17	5.54	0.43	5.0-6.3	14	5.66	0.46	4.9-6.6
SL(mm)	7			15-23				
SL1	7	6.36	0.59	5.2-7.0				
SR1	7	77.6	2.5	73-80				
SW1	7	5.29	0.28	4.8-5.6				

Zealand specimens, carpus and manus not distinct from each other, dactylus slender, slightly expanded at tip. Suckers on carpus biserial for proximal 1-2 rows, tetraserial distally; manal suckers moderately large, slightly smaller on New Zealand specimens, possess finger-like fleshy fringes on outer margins, better developed on marginal suckers (Fig. 5d, e); median manal suckers 1.1-1.5 times diameter of marginals; dactylus suckers small becoming minute at tip, decrease in size from ventral to dorsal rows; distal tip slightly expanded, small naked patch present between median sucker rows at tip. Aboral swimming keel arises along the carpus, expands distally and terminates abruptly at tip, keel slightly thickened along attachment to club. Trabeculate protective membranes well developed, arise along proximal portion of carpus, trabeculae broad, strong, arise between sucker bases, diffuse at edges of membranes; dorsal membrane terminates along proximal portion of dactylus, ventral membrane continues along dactylus to distal tip.

Sucker rings of carpus with 18-30 pointed or truncate teeth on complete circumference, larger and more pointed distally. Sucker rings of manus also with 18-30 sharp teeth, larger distally on median suckers and

marginally on marginal suckers; largest teeth of marginal suckers generally larger than those of median suckers. Sucker rings of dactylus with 22-26 sharp teeth, fewer on distal suckers, teeth larger on ventral suckers, larger on ventral aspects of all suckers; sucker rings of terminal expansion of dactylus lacking dentition. *Buccal membrane* with seven lappets supported by strong connectives, lateral lappets strongest, ventral lappets generally lowest; each lappet bears 0-9 small suckers each bearing 20-25 minute, truncate teeth, larger on distal margins. Buccal seminal receptacle present on oral surface between ventral lappets of females, very well developed; large, transversely grooved spermathecal pad is only partially enclosed by folds of buccal membrane, aboral tip of pad free but lies closely against membrane.

Upper beak (Fig. 6f) with rostrum sharply pointed, long, curved, width approximately equal to length; rostral margin and tip dark brown to black, dark pigmentation expanded posteriorly to rostral margin and jaw angle, remaining area of rostrum and hood lightly pigmented. Hood length about 4-6 times rostral length; wing length about 1.5-2.4 times rostral length, cutting edge of wing straight, irregularly serrated, a large tooth present near jaw angle. Crest curved, lateral

Fig. 6—*Sepioteuthis australis* Quoy & Gaimard; male, NMVF30876, 214 mm ML. a, left ventral arm. b, hectocotylied portion of left ventral arm. c, funnel organ. d, spermatophore. e, oral end of spermatophore. f, upper beak. g, lower beak. h, gladius.

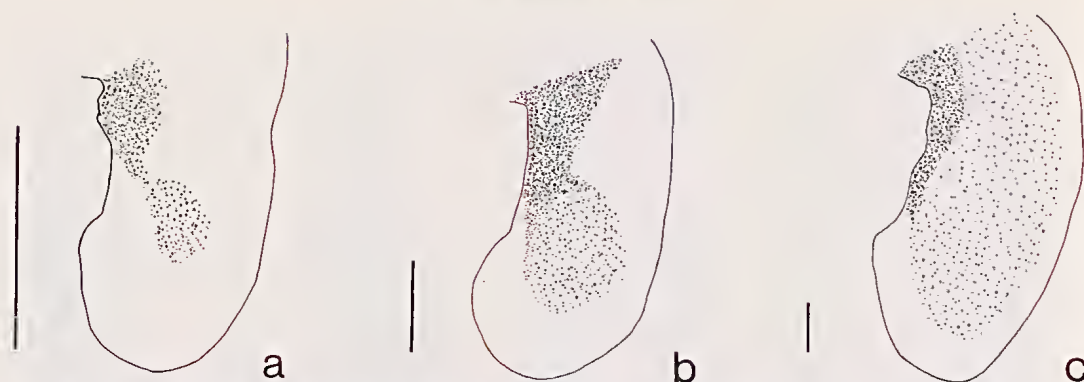


Fig. 7—*Sepioteuthis australis* Quoy & Gaimard. Development of darkening on beak wings. a, female, NMVF31567, 43 mm ML. b, male, NMNZM9829, 107 mm ML. c, male, NMVF30876, 214 mm ML. Scale bars equivalent to 2 mm.

wall large, lightly pigmented anteriorly on all specimens examined, posterior margin with a shallow indentation, lateral wall margin unpigmented. **Lower beak** (Fig. 6g) rostrum long, pointed, black, width approximately equal to length; cutting edge of rostrum straight, irregularly serrated. Wing 1.5–2.4 times rostral length, pigmentation occurs on animals of at least 43 mm ML: wing pigmentation (Fig. 7) begins as a lightly pigmented spot, expands gradually through a club shaped pigmented area, to the final stage of uniformly pigmented wing with transparent margins at about 200 mm ML. Hood heavily pigmented anteriorly, lightly pigmented posteriorly; crest curved, crest length about 3.0–4.5 times rostral length; lateral wall length about 3.5–6.0 times rostral length, lightly pigmented with transparent margins.

Radula (Fig. 5g) with seven transverse rows of teeth; rhachidian tooth stout with straight edges, lateral cusps high, sharp, slightly curved; first lateral about 90% of height of rhachidian, lateral cusp sharp, slightly curved; second lateral nearly straight, about 1.6 times height of rhachidian, stout, tip blunt, no cusps; third lateral curved, about 2.2–2.4 times height of rhachidian, tip blunt, no cusps; marginal plates ovoid. **Gladius** (Fig. 6h) broad, wider in New Zealand specimens; vane dilated posterior to attachment of funnel adductor muscles, widest at about half its length; thickened band immediately medial to vane edge extends from point of attachment of funnel muscles to posterior tip, vane edge unthickened. Free rachis short, moderately broad, strong, rounded central groove supported by thickened lateral rods which become weaker and disappear posteriorly.

Spermatophores (Figs 6d, e, 10) from the vicinity of the type locality with bipartite cement body; aboral end elongate, stout, slightly narrower orally; oral end of cement body connected to aboral end by a stout neck, flask shaped, tapering evenly or with a slight median bulge to oral extremity; oral extremity of cement body slightly dilated. Middle tunic commences along aboral part of cement body neck; may form two annular ridges along neck, strongly spirally sculptured along oral end

of cement body, less distinctly sculptured along ejaculatory apparatus. Ejaculatory apparatus strongly coiled, several coils in oral dilation of spermatophore. Badly damaged spermatophores from a single specimen from the northwestern extremity of this species range (WAM 785-81) still had intact cement bodies; these resembled specimens from southeastern Australia but had a slightly more elongate aboral end of the cement body. Spermatophores from New Zealand specimens (NMVF31752) similar in relative size to those from Australia, but with slight differences in the form of the cement body (Fig. 10b). Aboral end of cement body short, almost round, connected to oral end by a stout neck; oral end ovoid, lacking distinct shoulders adjacent to neck, oral extremity expanded. Middle tunic with a broad collar along cement body neck, lacks annular ridges, slightly constricted along oral end of neck; tunic spirally sculptured along oral end of cement body. Ejaculatory apparatus similar to Australian forms.

Specimens preserved in iso-propyl alcohol cream coloured; dorsal surface of mantle and fins closely covered in large, purplish chromatophores, more concentrated medially. Chromatophores on ventral surface of mantle less concentrated, ventral surfaces of fins lacking chromatophores. Specimens from northern limits of distribution generally darker coloured. Head and aboral aspects of arms and tentacles densely covered with small chromatophores, less concentrated ventrally; dark patches present over each eye. No photophores present in this species.

Males have well developed spermatophores in the needhams sac from about 200 mm ML. The smallest animal in which hectocotylisation could be observed was 79 mm ML. The nidamental glands of females begin rapid enlargement at 150–200 mm ML. As the largest male recorded was 355 mm ML and the largest females with large, egg filled ovaries were only 183 and 250 mm ML it seems likely that females do not achieve such a large size as males.

HOLOTYPE: MNHP 2.5.430. Sex unknown. 275 mm ML. Dried, fragmented remains of beaks only extant.

TABLE 4

COMPARISON OF MORPHOLOGICAL PARAMETERS OF *Sepioteuthis australis* FROM AUSTRALIA AND NEW ZEALAND

Regression data relating to Fig. 9. For explanation of abbreviations see Table 2. Regression coefficients in all cases are significant at the 0.1% level.

Ref. Fig. 9	Function	Sample	n	b	a	R ²	sig. diff.
a	MW-ML	Aust.	18	0.2446	2.4440	0.9827	p < 0.02 (slope)
		N.Z.	13	0.3057	2.7691	0.9395	
b	GW-ML	Aust.	18	0.1543	2.0862	0.9851	p < 0.001 (slope)
		N.Z.	14	0.2113	-1.1967	0.9860	
c	FW-ML	Aust.	18	0.6876	0.7665	0.9851	p < 0.02 (elev.)
		N.Z.	14	0.7665	2.4311	0.9635	
d	CL-ML	Aust.	18	0.3676	-3.9187	0.9868	p < 0.005 (slope)
		N.Z.	14	0.2893	1.4562	0.9446	
e	AS _I -ML	Aust.	18	0.0065	-0.0946	0.9692	p < 0.02 (slope)
		N.Z.	14	0.0052	-0.0417	0.9771	
f	AS _{II} -ML	Aust.	18	0.0092	-0.1443	0.9771	p < 0.002 (slope)
		N.Z.	14	0.0068	-0.0302	0.9539	
g	AS _{III} -ML	Aust.	18	0.0107	-0.1553	0.9821	p < 0.001 (slope)
		N.Z.	14	0.0074	-0.0466	0.9448	
h	AS _{IV} -ML	Aust.	18	0.0075	-0.0804	0.9573	p < 0.05 (slope)
		N.Z.	14	0.0059	-0.0109	0.9622	
i	CS-ML	Aust.	18	0.0163	-0.2635	0.9625	p < 0.001 (slope)
		N.Z.	14	0.0101	-0.0438	0.9195	

TYPE LOCALITY: Probably Western Port, Victoria.

DISTRIBUTION: *Sepioteuthis australis* is a neritic species around southern Australia, and northern New Zealand (Fig. 8b). The northernmost record on the west coast of Australia is from approximately 20°S, NW of Dampier (WAM 785-81); on the east coast it is from 27°40'S off Brisbane (NMVF31331). Bathymetric records range from 0-85 m. This species is common in sheltered southern waters such as Port Phillip Bay, Western Port, Gulf St. Vincent, and Spencer Gulf. In New Zealand the southernmost record is from 41°16'S, Nelson, Tasman Bay (Dell 1952).

GEOGRAPHIC VARIATION: Morphometric differences could be detected between southeastern Australian and New Zealand samples, by comparison of regressions of certain morphometric parameters plotted against mantle length (Fig. 9, Table 4). From Fig. 9a-c and Table 4, it is evident that New Zealand specimens are generally broader than those from SE Australia; this is reflected in the widths of the mantle, fins and gladius. The tentacular clubs of New Zealand specimens are also slightly smaller; this is reflected in the statistical differences in club length and club sucker diameter (Fig. 9d, i). Number of teeth on club suckers do not show any corresponding differences. Arm suckers on all arms are also smaller in New Zealand specimens (Fig. 9e-h), this is not reflected by any differences in number or form of the teeth on arm sucker rings. Other morphometric parameters compared which did not show any significant differences were head length, head width, fin length, and length of all arms.

Spermatophores from New Zealand also show differences to those from Australia (Fig. 10). New

Zealand specimens examined match closely in details of the cement body with the illustrations of Kirk (1884, pl. 6), which show the oral cement body without distinct shoulders at its junction with the cement body neck. These shoulders, giving the oral cement body a flask-like appearance are present in material examined from Western Australia, South Australia and Victoria, they are also evident in the illustrations of Verco and Cotton (1931).

REMARKS: Specimens of *Sepioteuthis australis* examined from Australia and New Zealand match closely with previous descriptions of *S. australis* by Quoy & Gaimard (1832, p. 77), Ferrusac & d'Orbigny (1834-48, p. 301). McCoy (1883, p. 27, Berry (1918, p. 249), Verco & Cotton (1928, p. 128) and descriptions of *S. bilineata* by Kirk (1884) and Dell (1952, p. 87). The similarity and probably conspecificity of *S. australis* from Australia and *S. bilineata* from New Zealand was pointed out by Adam (1939) and Dell (1952); however this is the first time that actual material from each locality has been compared. There do not appear to be any differences between Australian and New Zealand material examined which could substantiate separate species designations.

The name *Sepioteuthis bilineata* was introduced into New Zealand literature by Hutton (1880), a nomenclatural move which cannot be justified as his identification was based on the extremely poor type description of a specimen not originally from New Zealand, and which has been lost (Quoy & Gaimard 1832, p. 68). *Sepioteuthis bilineata* should be considered as a *nomen dubium* and the name *S. australis* applied to both Australian and New Zealand specimens.

The fragmented remnants of the beaks are all that remain of the type specimen of *Sepioteuthis australis*.

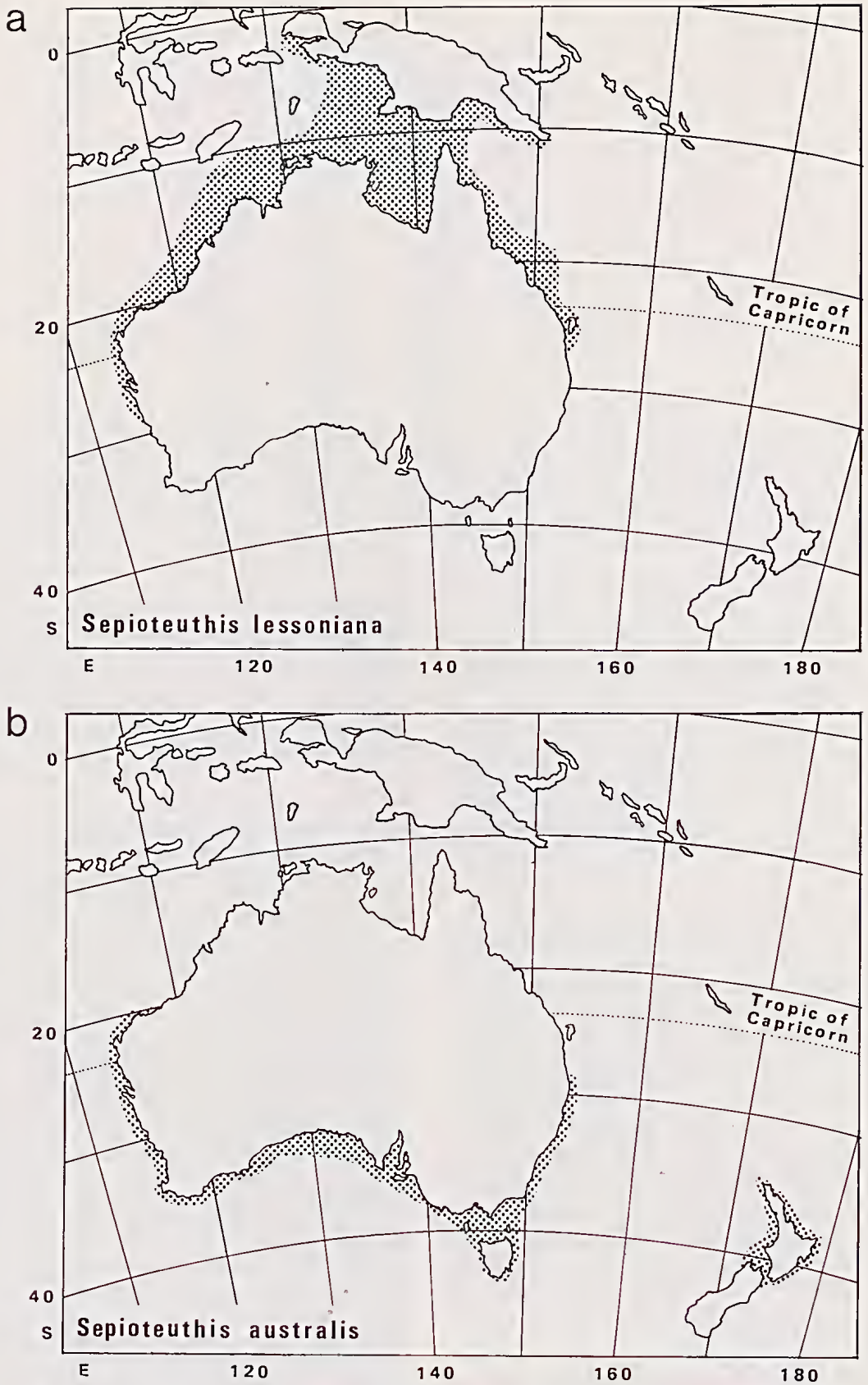


Fig. 8—a, distribution of *Sepioteuthis lessoniana* around Australia. b, distribution of *Sepioteuthis australis*.

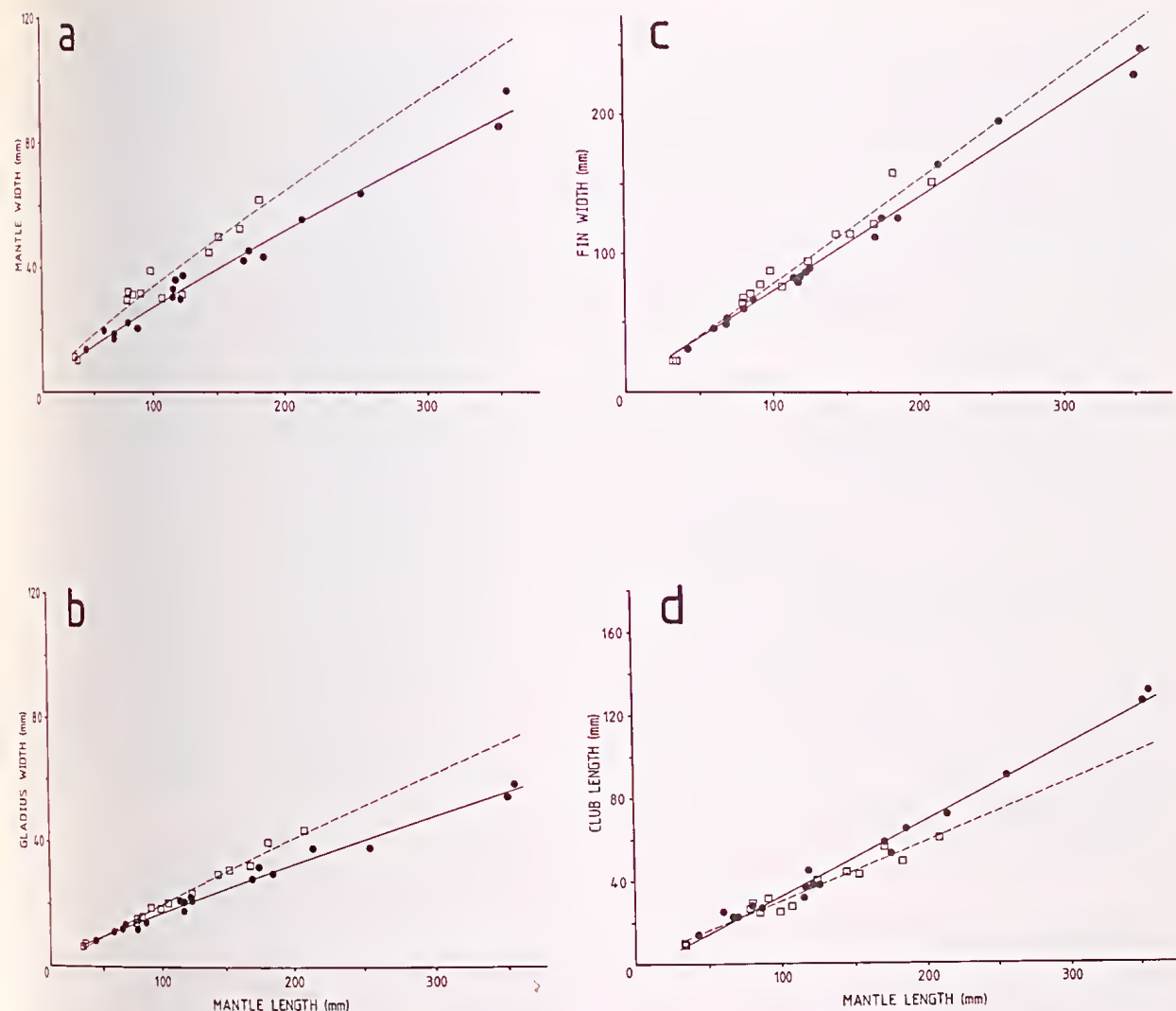


Fig. 9—Comparison of morphological parameters of *Sepioteuthis australis* from Australia and New Zealand. Australian sample—solid lines and solid dots. New Zealand sample—dashed lines and hollow squares. Regression data and comparisons of lines are given in Table 4.

These serve no useful taxonomic purpose; however, the complete type specimen was well described and illustrated by both the original authors and Férussac and d'Orbigny (1834-48).

Morphological differences which can be statistically detected between the Australian and New Zealand samples examined indicate that they are distinct populations. The New Zealand population is characterised by a relatively broader body, smaller tentacle clubs, smaller arm, and club sucker rings, and the spermatophore oral cement body lacking distinct shoulders. These differences are probably due to the isolating effect of the Tasman Sea on a neritic species.

DISCUSSION

Of the five species of *Sepioteuthis* recorded from Australia and New Zealand, only two are considered valid: *Sepioteuthis lessoniana* and *S. australis*.

Sepioteuthis lunulata of Brazier (1892) is a synonym of *S. lessoniana*. *Sepioteuthis mauritiana* described by Meyer (1909) from Albany, Western Australia is undoubtedly referable to *S. australis*. *Sepioteuthis mauritiana* is now known to be a synonym of *S. lessoniana*, but Meyer's illustration shows the fins of his specimen to be widest at their mid point. Further, Albany is far south of the recorded distribution of *S. lessoniana*, but well within the distribution of *S. australis*. This is in accordance with the opinion of Adam (1939, p. 28) as to the identity of Meyer's specimens. *Sepioteuthis bilineata* was poorly described from a single specimen from Western Port; no measurements were given and the poor illustration was evidently made from a quick sketch of a live animal. The inadequacy of the type illustration has since attracted comment by both Férussac and d'Orbigny (1834-48, p. 302) and Adam (1939, p. 30). The specimen was reported lost by the authors

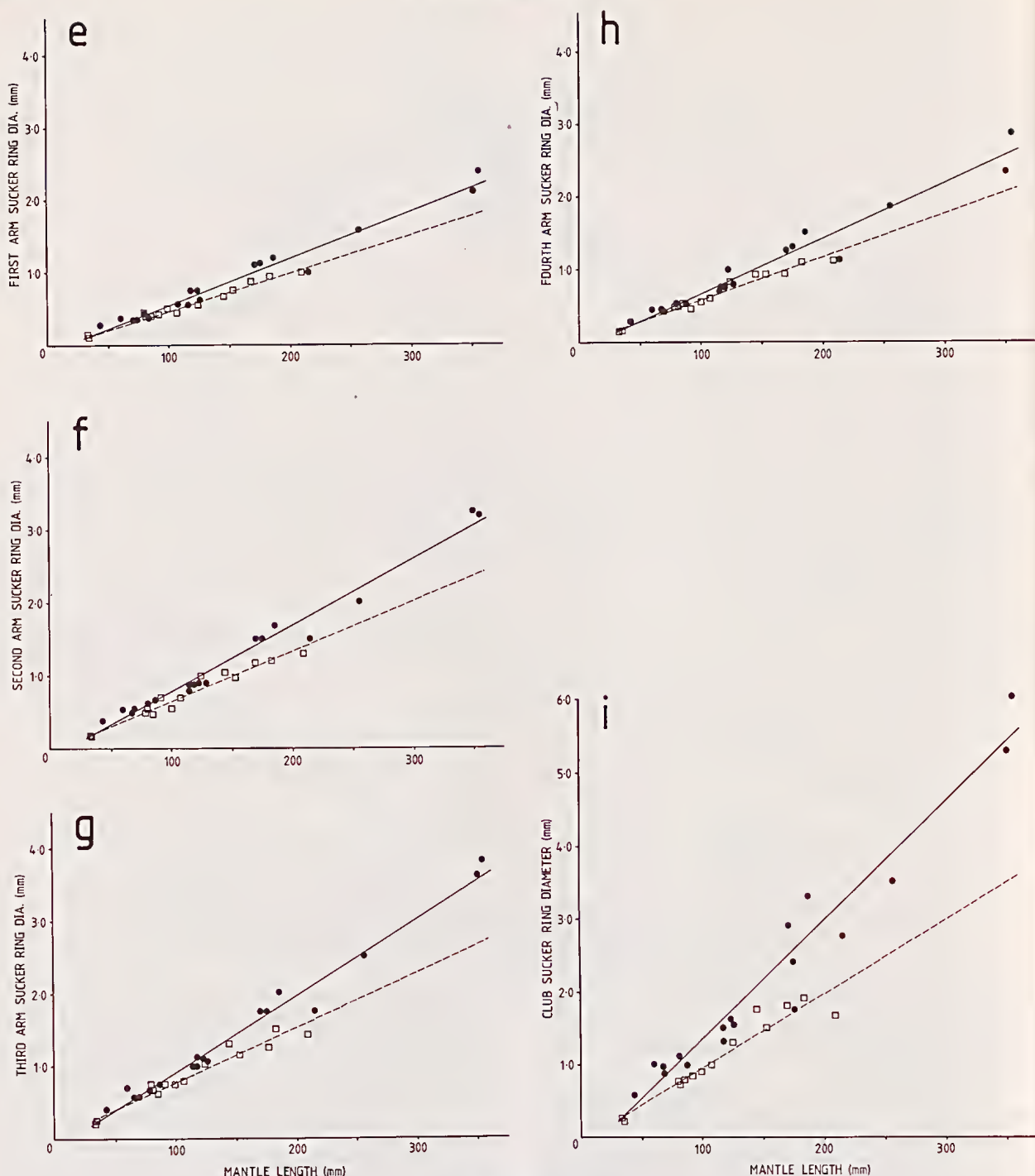


Fig. 9—(continued)

without any further information being available (Quoy & Gaimard 1832, p. 68). Dell (1952), based on Hutton's (1880) identification of the New Zealand species of *Sepioteuthis* as *S. bilineata*, submerged the name *S. australis* into synonymy with *S. bilineata*. This is impossible to justify in the absence of an adequate type description or type specimen of *S. bilineata*. Prior to

Dell, Adam (1939, p. 30) had already suggested *S. bilineata* to be 'a *nomen dubium*'—'comme le *Sepioteuthis bilineata* est très mal connu et que le type a été perdu (selon les auteurs), tandis que le dessin original est très douteux, je ne crois pas pouvoir l'accepter'.

The New Zealand species of *Sepioteuthis* can be positively identified as *S. australis*, the validity of which



Fig. 10—*Sepioteuthis australis* Quoy & Gaimard. Geographic variation in spermatophore cement bodies from Australia and New Zealand. a, NMVF30876, 214 mm ML, S.E. Australia. b, NMVF31752, 250 mm ML, New Zealand.

species may be established beyond doubt due to the adequate type description and subsequent description and illustration of the type specimen by Ferrusac and d'Orbigny (1834-48). The validity of *S. bilineata* however, cannot be established with any degree of certainty and we therefore agree with Adam that *S. bilineata* is a *nomen dubium* and that the species of *Sepioteuthis* from southern Australia and New Zealand is *S. australis*.

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APPENDIX 2 *continued*

	NMV F27004	NMV F31567	NMV F30852	NMNZ M74110	NMV F30241	NMNZ M5655	NMV F30851	NMV F31573	NMNZ M74106	NMV F30868	NMNZ M74106	NMNZ M74107	NMV F31574	NMV F30873	NMNZ M74117	NMV F31574	NMV F30876
Sex	M	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
ML	355	43	69	80	80	85	116	118	124	125	144	153	170	175	183	186	256
VML	318	41	56	72	67	78	97	105	114	112	130	125	149	151	164	167	221
MW	96	14	18	32	22	31	31	36	36	37	43	50	42	45	62	43	63
HL	67	9	17	22	18	17	23	29	26	29	29	32	40	32	41	38	58
HW	68	14	20	27	22	25	35	28	31	33	36	34	43	39	42	43	64
FL	320	36	61	70	72	73	104	107	113	120	130	132	151	158	167	175	225
FW	250	31	51	69	61	71	82	73	95	99	115	115	112	126	160	127	197
AL _I	108	10	15	23	20	18	28	32	30	29	36	34	39	44	44	48	63
AL _{II}	132	14	22	31	29	28	36	48	42	41	51	52	55	57	60	68	88
AL _{III}	153	18	28	38	36	39	46	53	51	49	61	62	66	67	70	80	97
AL _{IV}	134	18	28	39	37	37	47	52	48	48	53	56	70	65	67	76	102
HA	145																
HC	27																
TL	440	38	50	102	65	90	75	173	129	94	98	99	158	150	128	162	262
CL	131	14	23	29	28	25	32	45	40	38	44	43	59	53	50	65	90
AS _I	2.4	0.3	0.4	0.4	0.4	0.4	0.6	0.8	0.6	0.6	0.7	0.7	1.1	1.1	1.0	1.2	1.6
AS _{II}	3.2	0.4	0.6	0.6	0.6	0.5	0.8	0.9	1.0	0.9	1.1	1.0	1.5	1.5	1.2	1.7	2.0
AS _{III}	3.8	0.4	0.6	0.8	0.7	0.6	1.0	1.1	1.1	1.1	1.3	1.2	1.8	1.8	1.5	2.0	2.5
AS _{IV}	2.8	0.3	0.4	0.5	0.5	0.5	0.7	0.8	0.8	0.8	0.9	0.9	1.3	1.3	1.1	1.5	1.9
CS	6.1	0.6	0.8	0.8	1.1	0.8	1.5	1.8	1.3	1.6	1.8	1.5	2.9	2.4	1.9	3.3	3.5
GW	59	8	13	16	12	16	22	21	24	22	29	31	28	32	40	30	38
RL	66	10	13	14	15		22	22	22	22	28	26	30	31	40	30	46
RW	18	2	3	5	4		6	6	7	7	9	8	10	10	12	11	14
SL	23																
NL		3	7	7	8	10		21	16	13	26	46	19	13	56	22	90

APPENDIX 3

MEASUREMENTS (IN MM) OF UPPER AND LOWER BEAKS OF 10 SPECIMENS OF *Sepioteuthis lessoniona* FROM AUSTRALIAN WATERS

	NMV F31551	NMV F31549	NMV F31552	NMV F31547	NMV F31548	NMV F31576	NMV F31556	NMV F31611	NMV F31546	NMV F31557
Sex	F	M	M	F	M	M	F	M	F	M
ML	85	104	118	132	172	217	218	220	250	356
Upper Beak										
ROL	1.4	2.4	2.7	3.0	3.2	3.9	4.1	4.0	5.1	7.7
ROW	1.6	2.4	2.7	2.7	3.3	3.5	3.8	4.1	4.6	6.7
WL	3.2	3.8	3.8	4.2	6.5	7.2	9.4	9.2	9.1	14.5
HdL	8.0	11.0	10.5	11.8	15.0	18.5	21.2	18.5	20.6	28.5
LWL	10.4	13.2	14.0	15.1	20.8	24.3	28.0		27.2	40.3
Lower Beak										
ROL	2.1	2.5	2.6	2.7	3.0	3.9	4.3	4.3	5.1	6.9
ROW	2.0	2.5	2.9	3.0	3.3	4.6	5.0	4.6	6.3	7.0
WL	5.3	6.6	7.2	7.6	10.5	12.5	16.0	12.4	14.7	23.7
BL	8.0	9.2	10.5	11.0	14.7	18.5	18.6	18.7	20.5	28.0
D	6.7	7.4	7.3	7.7	11.0	12.7	17.0	12.7	14.0	20.6
HdL	2.9	3.5	3.6	4.3	5.7	7.1	8.0	6.6	7.4	11.4
CrL	6.6	8.5	9.0	9.7	12.9	15.5	17.5	15.0	17.7	25.5
LWL	8.0	10.7	10.4	11.2	14.4	17.6	19.6	17.7	20.0	28.3

APPENDIX 4

MEASUREMENTS (IN MM) OF UPPER AND LOWER BEAKS OF 14 SPECIMENS OF *Sepioteuthis australis* FROM AUSTRALIAN AND NEW ZEALAND WATERS

	NNNZ M21933	NMV F31567	NMV F31572	NNNZ M74110	NMV F30868	NNNZ M113321	NNNZ M9829	NMV F30868	NNNZ M74106	NNNZ M74106	NMV F30873	NMV F31574	NMV F30876	NMV F27004
Sex	M	F	M	F	M	M	M	M	F	F	M	F	M	M
ML	34	43	68	80	87	99	107	117	124	144	175	186	214	355
Upper Beak														
ROL	0.6	0.7	1.1	1.4	1.1	1.5	2.0	2.3	2.5	2.1	3.0	3.8	3.7	5.4
ROW	0.6	0.8	1.1	1.5	1.1	1.2	1.7	2.0	1.9	2.4	3.0	3.2	4.0	5.6
WL	1.0	1.7	1.8	2.4	2.4	2.8	3.0	4.5	4.1	4.6	4.9	6.4	6.5	9.0
HdL	2.7	3.9	5.2	6.8	6.9	8.7	8.5	9.6	10.7	12.0	15.3	15.2	15.5	23.8
LWL	2.7	3.9	4.8	6.0	6.7	7.8	6.5	9.0		11.3	15.0	16.2	14.0	24.6
Lower Beak														
ROL	0.5	0.8	1.0	1.4	1.1	1.3	1.8	2.2	2.5	2.3	3.1	3.7	4.0	6.6
ROW	0.6	0.8	1.1	1.7	1.1	1.5	1.7	2.0	2.5	2.4	3.4	3.7	4.0	7.0
WL	1.7	2.8	3.2	4.5	4.4	5.3	6.0	6.5	6.9	7.8	10.4	9.8	12.0	16.1
BL	2.5	3.8	4.9	6.7	6.7	7.8	7.2	8.6	10.7	12.0	14.4	15.0	13.5	21.0
D	1.6	3.0	4.0	5.3	5.2	4.8	5.5	8.0	7.0	7.3	11.0	11.2	11.7	19.2
HdL	1.0	1.4	1.7	2.3	2.2	3.3	3.0	4.1	4.1	4.6	5.3	6.0	5.6	7.4
CrL	2.2	3.1	4.3	5.6	4.8	6.2	5.8	7.8	8.2	10.0	13.0	13.0	12.4	19.0
LWL	2.6	3.7	5.1	6.6	6.8	7.8	7.0	9.5	11.0	11.2	14.3	15.5	14.0	22.0

APPENDIX 5

MATERIALS EXAMINED: *S. lessoniana*

No.	Sex	ML (mm)	Reg. No.	Location	Date	Depth (m)
1	M	104	NMV F31549	16°31'S, 145°43'E	7-V-1981	31
1	M	110	NMV F31554	14°10'S, 124°26'E- 14°09'S, 124°29'E	26-III-1981	93-95
1	M	118	NMV F31552	16°40'S, 145°39'E	7-V-1981	13-18
1	M	155	NMV F31555	19°30'-20°10'E, 155°50'-177°20'E	X1-1981	45-75
3	M	157-208	NMV F31553	20°10'S, 116°04'E- 20°10'S, 116°08'E	9-III-1981	60
1	M	172	NMV F31548	18°05'S, 121°47'E- 18°01'S, 121°48'E	26-V-1979	40-42
2	M	196-217	NMV F31576	21°21'S, 114°44'E- 21°19'S, 114°40'E	4-V-1979	82-98
2	M	220-270	NMV F31611	27°12'S, 153°05'E	12-IX-1980	
1	M	356	NMV F31557	23°55'S, 152°24'E	1-VII-1980	
1	F	85	NMV F31551	14°02'S, 124°36'E- 13°59'S, 124°36'E	23-III-1981	86
1	F	95	NMV F31550	20°14'S, 177°12'E- 20°14'S, 177°15'E	2-VI-1981	39-40
1	F	132	NMV F31547	12°18'S, 124°04'E- 12°19'S, 124°06'E	31-III-1981	80-91
1	F	155	NMV F31575	13°14'S, 125°07'E- 13°13'S, 125°05'E	30-III-1981	77
2	F	218-224	NMV F31556	27°10'S, 153°03'E	7-X-1980	
1	F	250	NMV F31546	20°00'S, 116°05'E- 20°03'S, 116°08'E	9-III-1981	62-66
10	M	72-259	NMV F31764	9°52'N, 123°09'E	X1-1979	
11	F	62-197				
1	M	112	ZMC	Nhatrang Fishmarket, Vietnam	7-X-1959	

APPENDIX 6
MATERIALS EXAMINED: *S. australis*

No.	Sex	ML (mm)	Reg. No.	Location	Date	Depth (m)
2	M	33-34	NMNZ M21933	35°13'S, 174°04'E	III-1967	
2	M	56-56	NMV F31331	27°40'S, 153°29'E	6-XI-1981	32
1	F	48				
1	M	60	NMV F24447	38°09'S, 144°23'E		
1	M	68	NMV F31572	40°00'S, 144°21'E	2-II-1981	47
				40°00'S, 144°26'E		
1	M	79	NMNZ M74110	41°17'S, 174°54'E	1-XII-1960	
1	F	80				
2	M	87-117	NMV F30868	40°31'S, 145°04'E	3-XI-1980	29
1	F	125				
1	M	91	NMNZ M11174	41°19'S, 174°48'E	10-IV-1957	
1	M	99	NMNZ M13321	41°16'S, 174°48'E	I-1959	
1	M	107	NMNZ M9829	41°19'S, 174°53'E	16-V-1959	7
2	M	114-208	WAM 785-81	c 20°S, 116°E		77-84
1	M	123				
1	F	116	NMV F30851	38°21'S, 145°13'E	25-III-1981	
1	M	169	NMNZ M17891	36°19'S, 175°29'E	1962	
1	M	175	NMV F30873	39°56'S, 144°48'E	3-II-1981	49
				39°54'S, 144°48'E		
1	M	209	NMNZ M74108	41°15'S, 174°50'E	XI-1952	
1	M	214				
1	F	256	NMV F30876	40°38'S, 145°23'E	4-XI-1980	36
4	M	250-300*	NMV F31752	c 41°S, 175°E	21/28-VII-1982	
1	M	300*	NMV F31753	38°32'S, 145°21'E	28-XI-1982	6
1	M	342	NMV F31756	38°32'S, 145°21'E	28-XI-1982	6
2	M	350-355	NMV F27004	38°17'S, 144°40'E	1882	
2	M	362-382	NMV F31755	Melbourne Fish Market	13-IX-1888	
1	F	43	NMV F31567	39°03'S, 146°29'E	10-II-1982	13
1	F	69	NMV F30852	Western Port Bay, Vic.	2-V-1967	
1	F	80	NMV F30241	38°21'S, 145°13'E	8-VI-1974	
1	F	85	NMNZ M5655	Wellington Hbr, N.Z.		
1	F	118	NMV F31573	34°55'S, 137°48'E	24-IX-1979	31
2	F	124-144	NMNZ M74106	34°59'S, 173°57'E	VII-1953	
1	F	153	NMNZ M74107	34°59'S, 173°57'E	I-1954	
2	F	170-186	NMV F31574	38°47'S, 146°45'E?	13-XI-1959	20
1	F	183	NMNZ M74117	35°14'S, 174°08'E	1960	
		268-280	NMV F31754	40°31'S, 145°04'E	3-XI-1980	29

* Indicates reproductive organs only examined.